

## Stimulation of Lake Michigan Plankton Metabolism by Sediment Resuspension and River Runoff

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**ABSTRACT.** Previous work during a major sediment resuspension event (March 1988) in southern Lake Michigan demonstrated that nutrients and carbon derived from resuspended sediment stimulated intense winter heterotrophic production while simultaneously decreasing light availability and autotrophic biomass. However, the role of riverine inputs on plankton metabolism remained unclear. Here we present results from a simulated enrichment experiment (March 2000) designed to examine the influence of resuspended sediments and riverine inputs on Lake Michigan plankton dynamics. Lake water amended with realistic levels of river water, coastal resuspended sediment and river water + sediment all showed enhanced heterotrophic bacterial production and plankton respiration rates, relative to the lake water control. Bacterial production increased by approximately 4× in river water treatments and by a factor of 2.5× for the sediment only treatment compared to lake water controls. Rates of net primary production were stimulated by river water (8.5×) and resuspended sediment (3×), but most by a combination of river water + sediments (11×). Community respiration showed a similar response with rates approximately 8× higher in river water amendment treatments and 3.5× higher in the sediment treatment. Extrapolating experimentally determined production rates to the southern Lake Michigan basin indicated that heterotrophic and autotrophic production in this nearshore region may be enhanced by as much as 3× and 5.2× due to these source inputs. Indeed, field measurements throughout southern Lake Michigan from 1998–2000 support these experimental results. Experimental and field observations suggest that both seasonal riverine inputs and episodic resuspended sediments influence the regional scale ecosystem metabolism and biogeochemistry in Lake Michigan.

**INDEX WORDS:** Sediment resuspension, river runoff, plankton metabolism, Lake Michigan.

### INTRODUCTION

Episodic, wind-induced, sediment resuspension events can have a profound influence on the biogeochemistry and trophic functioning of shallow lakes and coastal ecosystems (Schelske *et al.* 1995,

Eadie *et al.* 2002, Schallenberg and Burns 2004). Specifically, resuspension events can provide nutrients that have been regenerated within surficial sediments, inject meroplankton, benthic algae, and bacteria thus increasing planktonic biomass, and alter the availability of light within the water column. Previous bio-physical modeling experiments in southern Lake Michigan indicated that the spatial

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distribution of nutrients and the planktonic community were closely coupled to the physical environment associated with wind-induced circulation and mixing (Ji *et al.* 2002, Chen *et al.* 2002). Major resuspension events in southern Lake Michigan result from strong cyclones passing east of the lake, typically between October and April when the water column is unstratified (Mortimer 1988, Schwab *et al.* 2006). Detailed studies conducted under the Episodic Events Great Lakes Experiment (EEGLE) program verified that the scale of these events make them relevant for understanding patterns of nutrient distributions and planktonic productivity within southern Lake Michigan. For example, Eadie *et al.* (2002) estimated that amount of resuspended material within the basin following a single event was comparable to the total annual external load of fine-grained material, and that the material persisted within the water-column on the scale of a month. Similarly, Cotner *et al.* (2000) predicted that the increase in bacterial-associated phosphorus following a large resuspension event in March 1998 was more than twice the typical annual loading of phosphorus to the lake. Subsequent loss of this bacterial biomass, assumed through grazing and not settling, represented a re-introduction of nutrients into the food web equivalent to 34% of the external load or potential “new” production (“the ghost of production past”).

The impact of these large-scale resuspension events on phytoplankton production is less clear. Although resuspension events provide an additional source of nutrients, they also severely limit light penetration at a time of the year when incident radiation is low and mixing depths are deep due to unstratified conditions. Earlier field studies of phytoplankton responses during the resuspension events suggested that light saturated photosynthesis and growth rates were elevated in areas of the plume and positively correlated with increased dissolved phosphorus (Lohrenz *et al.* 2004). Further analyses, however, suggested that the source of the nutrients may well have been from river water contributions in the same area and model analysis suggested that reduced light availability from resuspension would actually suppress primary production during the spring season (Lohrenz *et al.* 2004). Collectively, regional rivers in the watershed annually discharge a volume of water that is approximately 0.5–1% of the volume of the southern Lake Michigan basin (Biddanda and Cotner 2002). The importance of river runoff as a nutrient and carbon source to fuel bacterial production and help

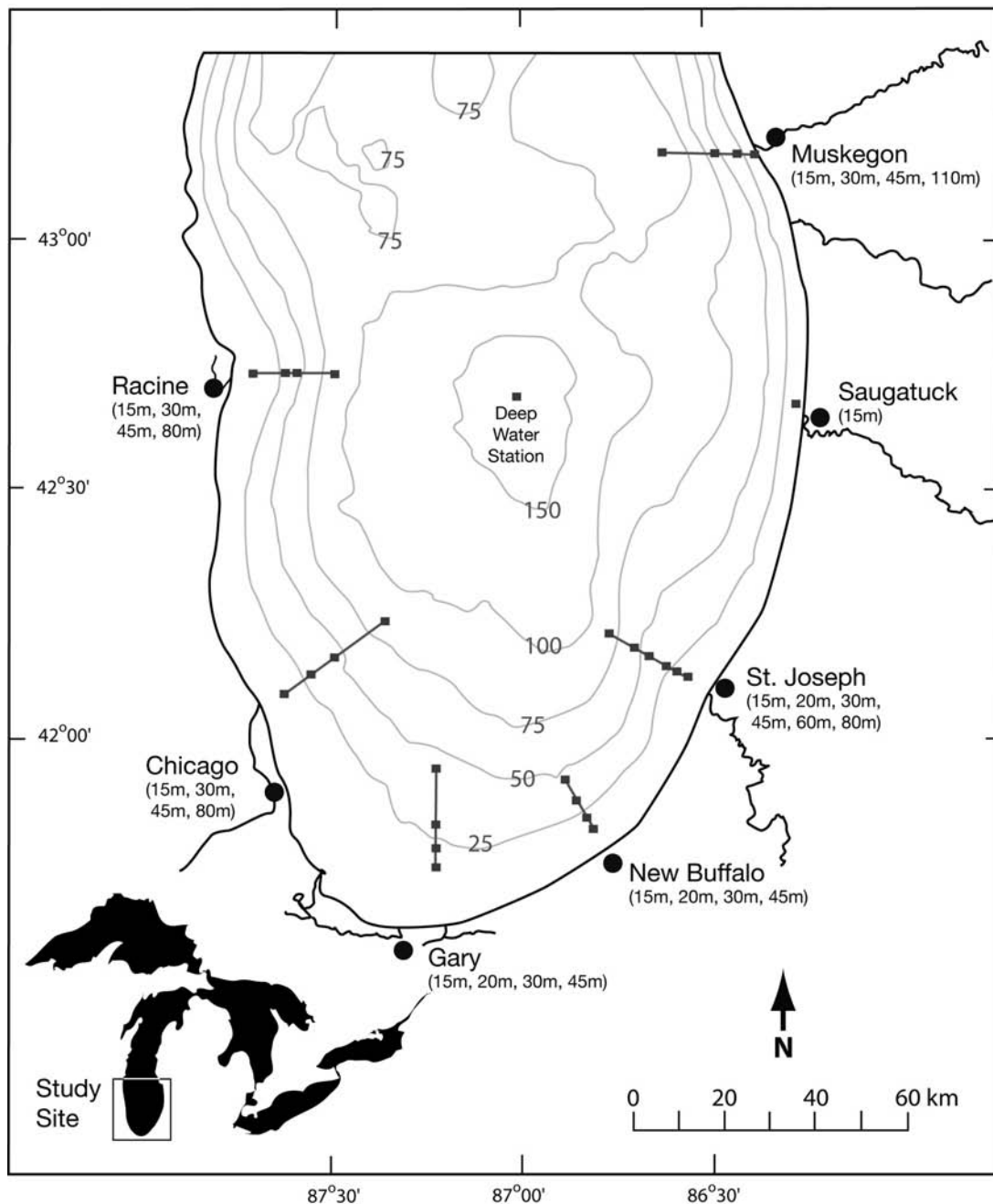
support seasonal imbalances between planktonic respiration and production was also described by Biddanda and Cotner (2002). In their study they estimated that terrigenous inputs via rivers could account for between 10–20% of the annual heterotrophy and autotrophy, respectively, in southern Lake Michigan. Research in other shallow ecosystems has also shown a mixture of sediment resuspension effects on phytoplankton production. Schallenberg and Burns (2004) found that primary production in the shallow lake systems studied always increased in response to resuspension, however, the effects seemed to be more closely tied to the introduction of meroplankton than from the direct input of limiting nutrients.

The goal of this study was to examine the influence of sediment resuspension and river runoff on lake plankton metabolism in the context of introducing biologically limiting nutrients such as phosphorus and metabolic substrate such as dissolved organic carbon. We examined results from controlled enrichment experiments to help isolate the individual and combined effects of these two processes, and to derive quantitative estimates of production and respiration in response to these inputs. The enrichment (“Home Brew”) experiment allowed for a direct comparison of both factors on the same water from direct measurement of rates for nutrient cycling and bacterial production. Here we describe results for nutrient assimilation, bacterial abundance, bacterial and primary production, and total planktonic respiration. We also provide a retrospective analysis of field observations collected over nearshore-offshore transects spaced throughout southern Lake Michigan during the 3 field years of the EEGLE project to examine the extent to which the impacts from resuspension and river runoff are expressed in nature. Patterns of productivity, biomass estimates, and nutrients observed in the field were compared against experimental findings. Lastly, we examine the potential importance of our findings in the regional context of the overall impact on productivity within southern Lake Michigan.

## METHODS

### Field Data

Twenty-seven cruises were conducted on an approximate monthly basis from 1998–2000 in southern Lake Michigan during the EEGLE study. Cruise tracks were organized around cross-shelf transects located throughout the southern basin (Fig. 1).



**FIG. 1.** Station depths and sampling locations for field observations collected during the 1998–2000 EEGLE study on cross-shelf transects within southern Lake Michigan.

Transects were selected to represent regions of varying bathymetry, substrate, and coastal influence. Complete basin surveys were conducted three times each year during winter, during resuspension events, and in early summer after stratification. Additional monthly-spaced cruises mainly sampled along the St. Joseph and Muskegon transects only. Data presented in this paper are restricted to

nearshore stations only, defined as having a water column depth of 30 m or less, to make the most direct comparison of field observations to our enrichment incubation experiment defined below.

At each sampling station the water column was profiled with a SeaBird STE-911 multi-sensor unit to determine the hydrographic structure. Discrete water samples were collected between 2–5 depths

**TABLE 1.** Means and standard deviation of nutrients concentrations, bacteria and biomass parameters from field samples collected in nearshore southern Lake Michigan (< 30m) during pre-stratification periods between 1998–2000 and in the St. Joseph River. Data were organized on the basis of observed total suspended matter (TSM) and chloride (Cl) concentrations as defined in Methods (BA = bacterial abundance, BP = bacterial production, TP = total phosphorus, TDP = total dissolved phosphorus, CHLa = chlorophyll a, POC = particulate organic carbon, DOC = dissolved organic carbon, n.d. = not determined).

	Riverwater (n = 1)	Lakewater Control Sites (n = 34)	Sediment Impacted Sites (n = 13)	River Impacted Sites (n = 11)	River + Sediment Impacted Sites (n = 10)
BA ( $\times 10^6/L$ )	n.d.	1.222 (0.511)	1.377 (0.458)	1.714 (0.822)	1.286 (0.457)
BP ( $\mu g\ C/L/d$ )	33.7	1.12 (0.82)	2.05 (1.80)	3.77 (3.21)	2.41 (2.19)
TSM (mg/L)	19.4	1.4 (0.8)	8.7 (5.1)	1.9 (0.6)	17.0 (14.6)
TP ( $\mu g/L$ )	85.7	5.2 (1.2)	9.8 (3.4)	8.2 (2.2)	22.2 (18.1)
TDP ( $\mu g/L$ )	27.6	1.8 (0.7)	2.4 (1.4)	1.8 (0.8)	3.0 (1.0)
CL (mg/L)	35.5	11.8 (0.9)	11.6 (0.6)	14.7 (1.8)	14.0 (1.0)
CHLa ( $\mu g/L$ )	18.4	1.29 (0.61)	1.11 (0.73)	2.60 (0.88)	2.43 (2.15)
POC (mg/L)	n.d.	0.19 (0.04)	0.28 (0.08)	0.30 (0.06)	0.49 (0.31)
DOC (mg/L)	n.d.	1.68 (0.40)	1.76 (0.52)	2.32 (0.48)	2.84 (2.12)

using Niskin bottles and processed immediately on the shipboard laboratory. Data were organized into four categories on the basis of both observed total suspended matter (TSM) and chloride (Cl) concentrations as follows: Lake water or control data were taken from sites where the Cl concentrations were within 10% of the deepwater offshore means (generated from stations between 45–150 m) and TSM concentrations were below 3.0 mg/L. Data for the sediment impacted zone were taken from sites where TSM was greater than 3.0 mg/L and Cl concentration remained within 10% of the offshore mean. Data for the river impacted zone were taken from sites where Cl concentrations were more than 10% greater than the offshore mean and TSM was below 3.0 mg/L. Data for the river + sediment im-

pacted zones were taken from sites where Cl concentrations were elevated by more than 10% from the offshore mean and TSM was above 3.0 mg/L. Means and standard deviations of nutrient concentrations, TSM, bacterial abundance, and bacterial production for these strata are given in Table 1.

### Enrichment Incubation Experiment

A cruise was conducted on 21 March 2000 to collect surficial sediment, offshore lake water, and river water to set-up a microcosm enrichment experiment. Lake water and sediments were collected at a 45 m deep station (NB45) located at 41° 57.20' N, 86° 48.58' W (Fig.1). This site was determined to be out of the direct influence of both river inputs and resuspension and thus served as the source for

**TABLE 2.** *Initial experimental conditions (mean and standard deviation) and river end member for enrichment incubation experiment (TSM = total suspended matter; Cl = chloride; TDP = total dissolved phosphorus; and DOC = dissolved organic carbon). TSM, Cl, and TDP values were determined from an initial composite solution that was subsequently distributed into triplicate treatment carboys. DOC values were determined from direct sub-samples of the triplicate carboys at the T0 timepoint.*

	Enrichment Treatments				
	River water	Lakewater	Sediment	River	Riv+Sed
TSM (mg/L)	15.0 (0.6)	1.2 (0.0)	34.1 (2.2)	5.3 (1.1)	38.3 (0.5)
Cl <sup>-</sup> (mg/L)	37.8 (0.9)	11.0 (0.1)	11.1 (0.0)	15.1 (0.0)	15.1 (0.1)
TDP (μg/L)	9.0 (0.7)	1.6 (0.0)	1.6 (0.0)	2.8 (0.1)	2.9 (0.1)
DOC (mg/L)	8.24 (1.07)	1.60 (0.10)	2.44 (0.49)	2.95 (0.43)	5.12 (0.99)

the open lake water control. Undisturbed surface sediments were collected with a box corer and then the top 0.5 cm aspirated from the surface into a clean vacuum flask. Sediments were composited from three box cores to collect sufficient material. Water was collected with 30-L Niskin bottles and transferred to polypropylene carboys and stored dark and cold until processed at the lab approximately 6 hr after collection. River water for treatment amendments was collected on the same day at the mouth of the St. Joseph River as the ship returned to port.

Following the cruise, the lake water, river water, and sediment suspension were transported back to the NOAA laboratory in Muskegon, Michigan for processing and distribution into the following four treatments: lake water control (Lakewater); sediment amended lake water (Sediment); river amended lake water (River); and, river plus sediment amended lake water (Riv+Sed). Each treatment solution was initially mixed in a 500 L plastic tank and then distributed to triplicate 12 L polycarbonate carboys. The Sediment treatment was created by adding sufficient extracted sediment to raise the TSM levels to approximately 30 mg/L, based on a percent transmission reading matched to previous field observations and later verified by direct measurement. The River treatment was created by adding 20% (by volume) river water to the lake water. The Riv+Sed treatment consisted of both extracted sediment and river water at the same proportions as for the individual treatments. Nutrient

concentrations (total dissolved phosphorus, TDP and dissolved organic carbon, DOC) in the river water were more than 5 times higher than the background lake water and approximately doubled these substrate concentrations in river amended treatments (Table 2). TSM levels in sediment amended treatments were approximately 30 times greater than for background lake water. All treatments were processed within approximately 2 hours from arrival at the laboratory, or 8 hours total from the time of initial field collection. The treatment carboys were then held in an outdoor rotating incubator at *in situ* temperatures, with light levels adjusted to 12% of spectrally matched incident irradiance (Lohrenz *et al.* 2004). Microcosms were sub-sampled immediately upon filling (T<sub>0</sub>) and then over a time-series covering 2, 4, 7, and 12 days for the final timepoint. Initial concentrations for TSM and dissolved nutrients were determined on replicate samples drawn from the composite treatment mixture immediately prior to distribution into triplicate treatment carboys due to the large volume requirement. All other estimates were taken on direct sub-samples from the triplicate carboys of each treatment.

### Analytical

Total suspended matter (TSM) concentrations were determined gravimetrically by filtering 1–2 L of lake water through combusted, pre-rinsed and pre-weighed 45 mm GF/F filters. Filters were weighed on a Mettler AT250 balance determined to

the nearest 0.1 mg. Chlorophyll *a* concentrations (Chl *a*) were determined by filtering duplicate 100-mL samples through a Whatman GF/F filter, freezing the filters until extraction with N, N-dimethylformamide (DMF, Speziale *et al.* 1984), and estimating pigments fluorometrically using the acid correction method (Strickland and Parsons 1972). Particulate organic carbon (POC), nitrogen (PON), and dissolved (DOC) organic carbon were determined by filtering through pre-combusted (4 h at 450°C) Whatman GF/F filters: DOC was determined by collecting the filtrate in pre-combusted glass vials, which were frozen prior to high temperature (680°C) combustion with a Shimadzu TOC 5000 carbon analyzer (Biddanda and Cotner 2002). Filters for POC and PON were frozen for preservation, acidified (1.0 N HCl) and dried prior to analysis on a Carlo-Erba model 1110, CHN elemental analyzer.

Nutrient and chloride concentrations were measured using standard automatic colorimetric procedures on an Auto Analyzer II after filtration freezing (0.2 µM nylon; Davis and Simmons 1979). Total phosphorus (TP) and total dissolved phosphorus (TDP) were stored in acid-cleaned Pyrex test-tubes in the refrigerator and then digested in an autoclave after addition of potassium persulfate (5% final concentration; Menzel and Corwin 1965) and then measured as for soluble reactive phosphate.

Bacterial abundance (BA) was measured on 5-mL samples that were preserved at a final concentration of 2% formaldehyde. Within 24–48 hours of collection 1-mL subsamples were stained with acridine orange and filtered onto a 0.2 µM black Poretics filter, mounted on slides and frozen. Abundances were determined on an epifluorescent microscope by counting a minimum of 300 cells and 20–40 fields of view (Biddanda and Cotner 2002).

Bacterial production (BP) was estimated from rates of protein synthesis using [<sup>3</sup>H]-leucine supplied at saturating values (20 nM) to quadruplicate 10 mL aliquots of lake water (3 live and 1 killed control [5% final concentration of trichloro acetic acid]) and incubated in the dark at ambient temperatures for 3 hours (Kirchman *et al.* 1985, Wetzel *et al.* 1995, Biddanda and Cotner 2002). Saturation and time-course curves were determined once each cruise and we confirmed saturation of radiolabel uptake at below 20 nM leucine levels as well as linearity uptake over the 3 hour duration of the incubation. Leucine incorporation was converted to

bacterial carbon production using a standard theoretical conversion factor of 2.3 kg C per mol of leucine (Simon and Azam 1989, Wetzel *et al.* 1995). BP rates presented herein are means from measurements determined for sampling time points on 0, 2, 4, 7, and 12 days, for each triplicate of each treatment, thus represent the overall average for the incubation period.

Net primary production (PP) was estimated from the measured rate of POC accumulation over time ( $\partial$ POC) after correcting for concurrently measured heterotrophic bacterial production rates (PP= $\partial$ POC-BP). Rates of PP were based on the difference in POC measured at the end of the 12 day incubation for each triplicate of each treatment, from the initial POC concentrations measured at T<sub>0</sub>, thus represent the overall average for the incubation period.

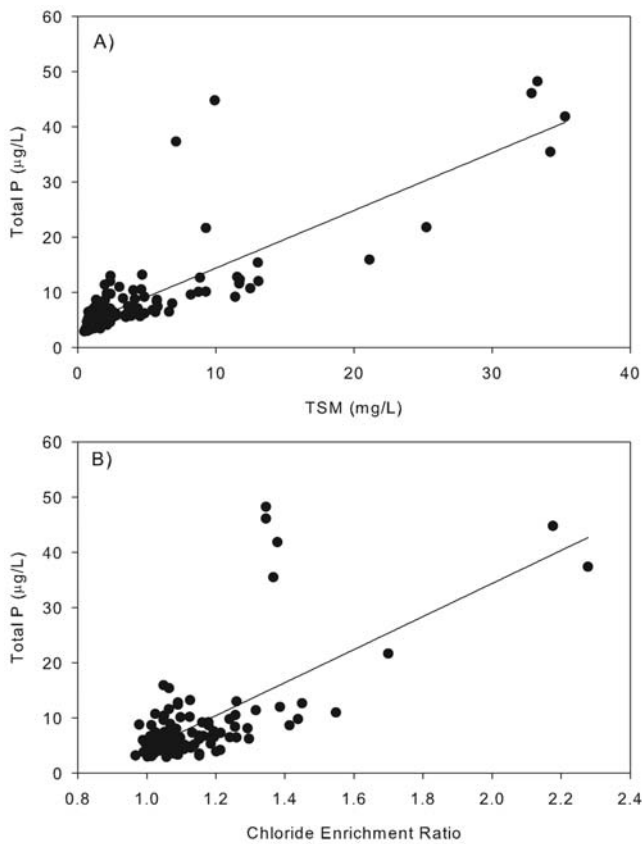
Total planktonic community respiration (CR) was measured by following changes in dissolved oxygen in 300 mL BOD bottles during dark incubations over a 4 d period at *in situ* temperatures (Biddanda and Cotner 2002). Rates were derived from a linear regression of DO concentrations determined at day 0, 1, 2, and 4. Dissolved oxygen measurements were made by automated Winkler titration based on potentiometric end-point detection using a Mettler DL-21.

Regression statistics were conducted using SYSTAT v11.0. Field observations were confirmed to be normally distributed according to Chi-square, Kolmogorov-Smirnov, and Shapiro-Wilk tests (all with  $p < 0.001$ ) prior to use in regression analyses.

## RESULTS

### Field Observations

Sediment resuspension and riverine inputs both contribute significantly to the supply of nutrients and DOC in the nearshore zone of Lake Michigan. Phosphorus and DOC concentrations in the major rivers surrounding southern Lake Michigan were typically 5–10 times greater than in the open lake (Tables 1 and 2; Cotner and Biddanda 2002). Chloride concentrations were also significantly enriched in river water (Tables 1 and 2) and we can estimate the potential importance of river input (and associated phosphorus) within the nearshore zone by examining the distribution of this conservative ion. The regression between total phosphorus and Cl concentrations was highly significant ( $p = 0.001$ ), but the predictive power was rather low ( $R^2 = 0.46$ ) due to a subset of data with very high TP concentrations (Fig. 2a). These outliers can be readily ex-



**FIG. 2.** Regressions of total phosphorus concentrations against (A) total suspended matter and (B) chloride concentration for field data collected within the nearshore zone of southern Lake Michigan from 1998–2000 as part of the EEGLE study.

plained on the basis of the other major process that regulates phosphorus concentrations, namely resuspension. Most phosphorus was associated with particulate matter and hence we observed a strong relationship between TP and TSM ( $p = 0.001$   $R^2 = 0.70$ ). Multiple regression demonstrated that 90% of the variance in TP concentrations in this nearshore environment was explained by a combination of TSM and Cl concentrations (Fig. 2b,  $R^2 = 0.90$ ,  $p = 0.001$ ).

To distinguish between the effects of resuspension and river inputs, field observations were organized on the basis of observed TSM and Cl concentrations relative to lake water controls (Table 1). Nutrient concentrations, planktonic biomass estimators, and heterotrophic production were compared on cross-shelf gradients that extended from depth contours between 10–30 m, including a direct

river sample on one occasion. Data within the sediment category represented sites influenced by high resuspension (average TSM was 6.2 times greater than for lake water), but showed no influence from river water on the basis of having Cl concentrations comparable to that for offshore lake water. Data within the River and Riv+Sed categories represented sites highly influenced by river inputs (average Cl concentrations between 20–27% above lake water, Table 1), but Riv+Sed data included samples that were also collected during periods of high resuspension (average TSM was 12× higher than lake water, Table 1).

River water contained roughly 3 times as much DOC and 10 times as much TP and TDP as offshore lake water (Table 1 and 2). Bacterial production (BP) in river samples was over 30 times greater than for lake water and chlorophyll concentrations were over 14 times greater. For sediment resuspension sites, mean BP rates were 83% higher than for control sites, despite only a minor increase in bacterial abundance. Dissolved phosphorus and DOC showed smaller increases (33% and 5% respectively), probably reflecting the fact that these inputs were utilized rapidly. Chlorophyll concentrations were lower at sediment sites than for open lakewater sites. For river only impacted sites, mean BP rates were 3.4 times higher than those for lakewater sites and bacterial abundance was 40% higher (*Field Observations*, Table 3). Again TDP and DOC showed less difference, 0 and 40% higher than lakewater sites. Chlorophyll concentrations were also 2.1 times greater at river sites, presumably a reflection of high nutrient inputs and low resuspended sediment particles. The Riv+Sed

**TABLE 3.** Enhancement Factor: Summary of increased bacterial production, primary production and community respiration rates in experimental enrichment treatments and in field observations (sediment resuspension and river runoff impacted coastal areas) relative to lakewater controls.

Treatment	Sediment	River	Riv+Sed
<i>Enrichment Experiment</i>			
Bacterial Production	2.43	3.74	3.90
Primary Production	3.32	8.56	11.14
Community Respiration	3.57	8.23	6.49
<i>Field Observations</i>			
Bacterial Production	1.83	3.37	2.15

**TABLE 4.** Carbon mass balance for each of the enrichment treatments after 12 days of incubation (Values represent mean and standard deviation of triplicates;  $\partial$ POC = change in POC over time, BP = bacterial production, PP = primary production =  $\partial$ POC-BP, CR = community respiration; P/R ratio was estimated as PP/CR).

	Enrichment Treatments			
	Lakewater	Sediment	River	Riv+Sed
$\partial$ POC ( $\mu\text{gC/L/d}$ )	11.17 (3.55)	35.25 (5.61)	85.67 (14.53)	109.50 (2.20)
BP ( $\mu\text{gC/L/d}$ )	2.06 (0.84)	4.99 (0.68)	7.68 (1.15)	8.01 (1.96)
PP ( $\mu\text{gC/L/d}$ )	9.11 (2.74)	30.26 (3.63)	77.99 (2.38)	101.49 (3.43)
CR ( $\mu\text{gC/L/d}$ )	10.08 (5.76)	36.00 (8.04)	82.92 (17.28)	65.40 (21.84)
P/R	0.90	0.84	0.94	1.55

designated sites showed a mixture of effects relative to only resuspension or only river inputs. Mean BP rates and chlorophyll concentrations were considerably higher than for lake water and moderately higher than for sediment sites, but lower than River only sites. TP, POC, and DOC concentrations behaved more conservatively and were the highest at sites influenced by both sources of input.

### Enrichment Experiments

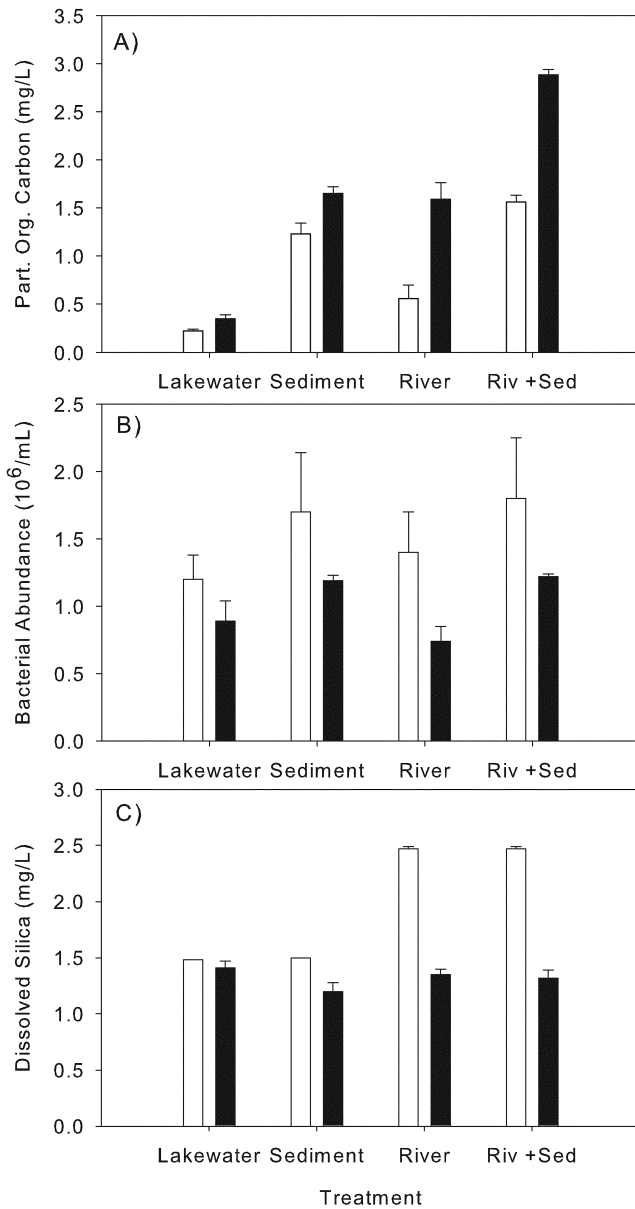
TSM concentrations in the Sediment treatment and Riv+Sed treatment were elevated to levels slightly greater than 30 mg/L, similar to the maximum levels observed in field samples during resuspension events (Table 2). Addition of river water roughly doubled TDP and DOC concentrations (Table 2). As expected, increases in TSM and DOC were additive for the Riv+Sed treatment, but TDP only increased to the same level as for river amendment alone, indicating that little TDP was provided by resuspended sediment.

Samples collected after 12 d of incubations indicated that planktonic metabolism and abundances responded significantly to treatments (Table 3). There were significant differences in the amount of POC accumulation among the four treatments (Fig. 3a). POC accumulated at rates 3.2, 7.7, and 9.8 times greater for Sediment, River, and Riv+Sed treatments, respectively, relative to controls (Table 4). Bacterial abundance initially increased by 42

and 12 percent respectively for the Sediment and River amendments, and decreased subsequently over time to approach levels in the Lakewater control (Fig. 3b). Despite the latter reduction in abundance, averaged bacterial production rates were significantly enhanced in all the treatments relative to Lakewater (see Fig. 4b and Table 4).

Dissolved silica concentrations were significantly increased in the river amended treatments relative to the control ( $2.47 \pm 0.02$  mg/L vs.  $1.48 \pm 0.00$  mg/L) but were unchanged in the sediment treatment ( $1.50 \pm 0.00$  mg/L) (Fig. 3c). All of the additional silica contributed from the addition of river water was assimilated over the course of the 12 d incubation likely due to stimulation of diatom production. Rates of silica assimilation ( $11.8 \pm 2.9$ ;  $43.6 \pm 1.9$ ;  $44.8 \pm 2.8$   $\mu\text{gSi/L/d}$ ), were 3.8, 14.4, and 14.8 times greater for Sediment, River, and Riv+Sed treatments, respectively, than in Lakewater ( $2.6 \pm 2.2$   $\mu\text{g Si/L/d}$ ). It appears that high sediment concentrations in the incubation experiment did not restrict autotrophic production as the amount of enhanced primary production in the Riv+Sed treatment was slightly higher than that for the River water treatment alone. Assuming that all of the silica was assimilated via diatom growth, and a C:Si mass ratio of 1.2 (Strickland 1965), then the accumulation of "diatom" carbon accounted for 23, 26, 44, and 35 percent of the total POC accumulation. Heterotrophic production and non-diatom au-

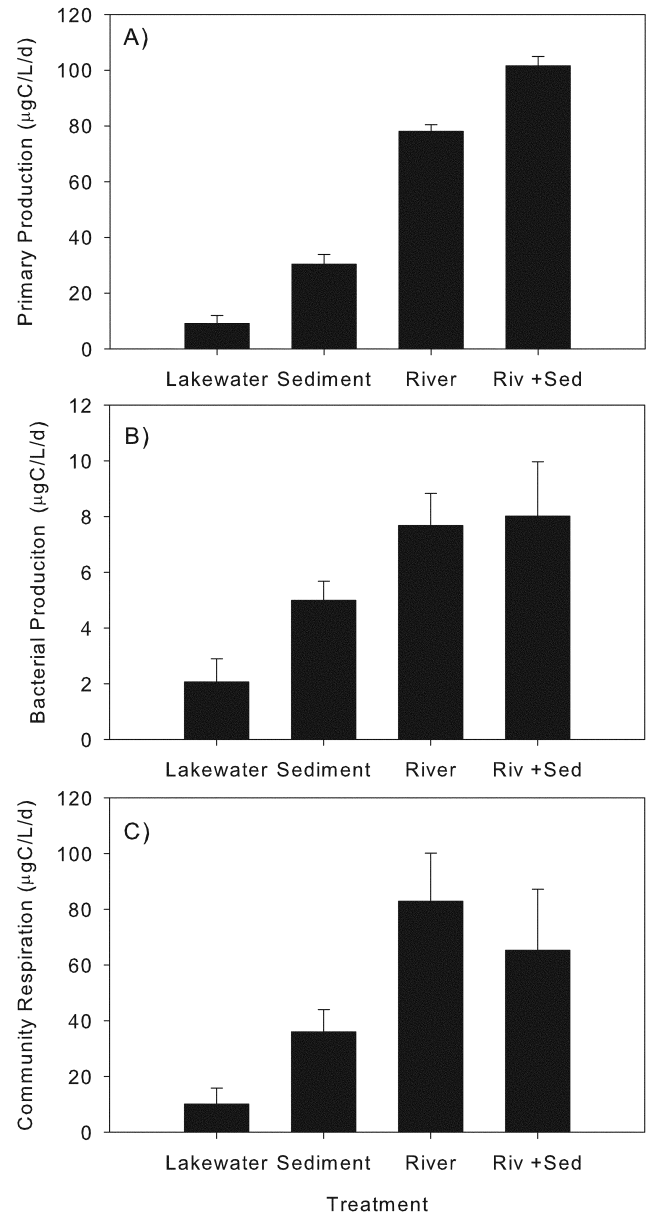




**FIG. 3.** Comparison of changes in particulate organic carbon concentration (A), bacterial abundance (B), and dissolved silica concentration (C) over the course of 12 day incubation for each of the enrichment treatments. Clear bars represent values on day 1 and solid bars represent values on day 12. Error bars represent 1 standard deviation ( $n = 3$ ).

totrophic production likely accounted for the rest (see below).

Metabolic processes (PP, BP, CR) were enhanced in all three amended treatments relative to Lakewater controls but river amended treatments again



**FIG. 4.** Summary of metabolic rates within experimental treatments in incubation enrichment experiments for estimated primary production (A), bacterial production (B), and community respiration (C). Error bars represent 1 standard deviation ( $n = 3$ ).

showed the greatest impact on rate measurements (Fig. 4, Tables 3 and 4). Specifically, estimated net primary production rates were 3.3, 8.6, and 11 times greater for sediment, river, and Riv+Sed treatments, respectively, than in Lakewater. These changes reflect an additive effect for the river and sediment inputs, again indicating that light limita-

tion was not a significant factor in the incubations. On average, the increase PP rate for river water amendments was nearly 3 times greater than for the sediment amendment. Similar results were observed for heterotrophic production rates, where BP was 2.4, 3.7, and 3.9 times greater for Sediment, River, and Riv+Sed treatments, respectively, than in lake-water controls (Fig. 4b). In the case for BP, differences between river and sediment treatments were much less, with average rates for River treatments only 60% greater than for Sediment treatments.

These experimental results were actually quite similar to the observed differences in BP rates for field samples in the nearshore zone of southern Lake Michigan (Tables 1 and 3) except that field results for the Riv+Sed sites were about half those observed in the incubation experiment. This contrast is not surprising given the fact that field observations represent time-averaged conditions versus experimental short-term addition of limiting substrates. Furthermore, the relatively high light conditions experienced in the incubations likely contributed to increased organic carbon availability to bacterioplankton due to high rates of PP. Lastly, community respiration rates (CR) were also significantly enhanced in all treatments (Fig. 4c), ranging 3.5–8.3 times higher than Lakewater—more or less in step with the enhancement in rates of PP (Table 3). It is unclear why the Riv+Sed treatment exhibited lower than expected rates of CR, but they may help explain the observed enhancement of net PP.

### Basin-scale Extrapolation

We carried out carbon mass balance estimates for each of the treatments by comparing rates of organic carbon accumulation, bacterial and autotrophic production, and community respiration (Table 4). Estimated primary production was 4.4, 6.1, 10.1, and 12.7 times greater than bacterial production in Lakewater, Sediment, River, and Riv+Sed treatments, respectively and accounted for between 80–90 percent of the accumulated organic carbon. River water amendments produced a greater effect than sediment input for both BP and PP, and the differences in the magnitude of response for these two types of input was greater for PP. Changes in CR tended to track with those for PP and BP and estimated P/R ratios (Table 4) were close to 1.0, with the exception for the Riv+Sed treatment which had a ratio of 1.55. This higher ratio appears to have been caused by a combination

of enhanced primary production rate and reduced CR rate in the Riv+Sed treatment.

We scaled the BP and PP rates observed in the enrichment experiments to the time and space scales for which these inputs have shown to be important in southern Lake Michigan from previous field studies. We assumed that resuspension may be present in the nearshore zone for 60 d per year (based on prior EEGLE field studies and Schwab *et al.* 2006 study on the frequency of resuspension events) and that the volume of water that would be impacted by river runoff was equal to five times the total annual river discharge (i.e., representing a 20% volumetric contribution to lake water and equivalent to the level of our river water amended treatments) for all major rivers draining to southern Lake Michigan. BP and PP rates were then computed for the nearshore region of southern Lake Michigan given each of the effects independently, and then as completely additive; i.e., without considering any negative interaction of sediment in river impacted zones (Table 5). These rates were compared against estimates using the rates from the Lakewater control, representing no river inputs or resuspension occurring in the nearshore zone. Overall, predicted BP in the nearshore zone of southern Lake Michigan was roughly 3-times higher (0.34 vs. 0.11) than it would have been without the two inputs. The production from sediment impacted regions contributed 38% of the total compared to 62% for the river impacted regions. Similarly, predicted PP in the nearshore zone was over 5-times higher (2.41 vs. 0.46) in the nearshore zone because of the two inputs. Again production in the sediment impacted zone accounted for only 26% compared to 74% for river impacted production. The nearshore zone of southern Lake Michigan is approximately equal to 7% of the volume of the entire basin, and further extrapolation to this regional scale implies a boost to BP and PP of 16 and 30% respectively as a result of inputs from river runoff and resuspension.

### DISCUSSION

Overall, these results confirm that both riverine inputs and sediment resuspension stimulated primary and secondary production in the nearshore region of Lake Michigan. While experimental results were derived from a single river and surficial sediment manipulation, the conditions of these end members were very typical of springtime conditions for Lake Michigan and therefore meaningfully represent the importance of these ecosystem drivers.

**TABLE 5.** Annual carbon production rates ( $10^9$  kg C/yr) for the nearshore zone of southern Lake Michigan (assuming mean depth = 25 m, shoreline length = 300 km, and distance offshore = 14 km). Rates are based on present enrichment incubation experiment and assuming 60 days of resuspension and a river impacted volume equal to 5 times the total annual discharge of rivers draining into the region (BP = bacterial production, PP = primary production).

Nearshore Zones	Annual Production ( $10^9$ kg C/yr)	Enhancement Ratio of Impact Rate to Control Rate
Sediment impacted BP rate	0.13	1.18
River impacted BP rate	0.21	1.90
Cumulative impact on BP rate	0.33	3.00
Sediment impacted PP rate	0.63	1.37
River impacted PP rate	1.79	3.89
Cumulative impact on PP rate	2.41	5.24
Lakewater Control BP rate	0.11	—
Lakewater Control PP rate	0.46	—

An important conclusion from these experimental and field results is that PP was stimulated in experimental treatments due to increased nutrients and sufficient light levels but this stimulation has not been observed *in situ* likely due to the negative effects of resuspended particles on water column light levels. On the other hand, microbial processes (BP and respiration) were stimulated by both riverine and resuspension inputs and this has been verified *in situ*, suggesting that increased net heterotrophy during this period could have important consequences for the net export of organic matter to offshore and deepwater regions of the lake.

### Enrichment Experiments

Results from the enrichment experiment confirm expectations that both river inputs and resuspended sediment stimulated production in the lower food web, including bacterial production, primary production, and community respiration. Riverine inputs produced a significantly greater stimulation of measured biological processes than did sediment input alone, however, in most cases there was an additive effect of sediment and riverine inputs suggesting that both likely play an important role in the natural setting. The combined input of these two factors (Riv+Sed treatment) produced stimulation in PP and BP that led to nearly a ten-fold increase in POC accumulation. The additive effect could reflect the fact that this treatment supplied the highest amounts of phosphorus and DOC, and also that the

inputs were an additional source of both bacteria and meroplankton as suggested by the initial bacterial abundance, POC, and chlorophyll values for river and sediment amended treatments (Fig. 3; Table 3 of Lohrenz *et al.* 2004).

Additional evaluation of our results can be made by comparing them to companion measurements on phytoplankton photosynthesis and growth reported by Lohrenz *et al.* (2004). Their reported treatment effects on photosynthetic parameters, chlorophyll and carbon specific growth rates on day 1 of the experiments were consistent with our findings. For example, they reported that chlorophyll was enhanced in all treatments: high in the sediment, even higher in the river only treatment, and highest in the river plus sediment treatment and P-turnover times were high in all treatments (6–7 hours). However, after 12 days of incubation, treatment effects on photosynthetic rates and carbon specific growth rates were minimal and P-turnover times decreased by about a factor of 10 suggesting that many of the treatment effects were proportional to increased P-availability that was subsequently consumed. It seems likely that initial stimulation of productivity via P addition associated with either sediments and/or river water were responsible for the increased biomass that accumulated in our experiments. Schelske *et al.* (1984) described similar experimental results to those reported by Lohrenz *et al.* (2004) wherein a 10% addition of Grand River (MI) water to lake water yielded a doubling of chlorophyll over a 7 day period. However, the stim-

ulation did not continue over a second week of incubation presumably because nutrients became depleted or because grazers responded on slower time scales than did the autotrophs.

Autotrophy and heterotrophy represent fundamental and complementary phenomena in ecosystems, and the balance between production and respiration is an essential descriptive feature of ecosystems (Biddanda *et al.* 2001, del Giorgio and Williams 2005). In the present study, riverine input stimulated autotrophic production to a greater extent than bacterial production. The ratio of bacterial to primary production (BP:PP) was 0.23 for Lake-water but decreased to only around 0.10 for river amended treatments. These results follow the general pattern for most aquatic systems in that bacterial production plays a greater role in oligotrophic conditions and autotrophic production becomes increasingly important as the degree of nutrient enrichment increases (Legendre and Rassoulzadegan 1995, Cotner and Biddanda 2002). Biddanda and Cotner (2002) previously reported that terrigenous subsidies provided by riverine input was significant in terms of carbon and phosphorus and could support approximately 10% of the carbon processed by bacteria and 20% of phosphorus associated with primary production for the southern Lake Michigan region. A carbon mass balance based on BP, PP, and CR for the enrichment treatments showed that both production and respiration were stimulated by the nutrients provided by river and sediment sources. The P/R ratio remained close to 1.0 in all of the treatments except the Riv+Sed, where the stimulus to production significantly exceeded respiration ( $P/R = 1.55$ ). This treatment had the highest concentration of nutrients which likely contributed to an increased growth of phytoplankton in the Riv+Sed treatment that presumably was not observed in the other treatments. Another possibility is that higher P/R in this treatment was observed because organic matter associated with the resuspended sediments and river water was rendered more bioavailable due to sunlight exposure (Biddanda and Cotner 2003), increasing bacterial growth efficiency and decreasing community respiration rates—while simultaneously enhancing primary production by autotrophic plankton due to increased availability of inorganic nutrients supplied by sediment and river water. These experimental results suggest that the river plume plus resuspended sediment complex could transport and fuel significant late winter autotrophic and heterotrophic production in the lake as recurrent

episodic storms drive nearshore water masses offshore.

### Comparison to Field Studies

Examination of EEGLE field data, using TSM and Cl concentrations as proxies of the relative influence of river inputs and resuspension, also indicated that river runoff had a much greater positive impact on bacterial production rates and chlorophyll biomass than sediment resuspension. The strong effect of river input follows logically from the significantly higher amounts of phosphorus and chlorophyll associated with the river water and the well-established role of phosphorus as the most critical limiting nutrient in the lake (Schelske and Stoermer 1972, Scavia and Fahnenstiel 1987). At sites experiencing high river runoff, bacterial production was over 3-times greater and chlorophyll concentration over twice those measured at non-impacted sites. In contrast, chlorophyll concentrations were lower for sediment impacted sites compared to open lake water. The patterns in chlorophyll were consistent with the previous findings of Millie *et al.* (2003) who concluded that while sediment resuspension altered the general composition of the phytoplankton community, there was no evidence for a significant increase in photosynthetic potential or growth rates at resuspension sites. Furthermore there was no evidence that bloom forming species typically of the spring bloom were taking advantage of increased nutrient availability. In contrast to an apparent lack of phytoplankton response in the field data, bacterial production was approximately 80% higher at sediment only impacted sites. Competition for available phosphorus by bacteria and rapid reaction rates with particles could suppress the potential stimulus of resuspension events on phytoplankton communities (Currie and Kalff 1984, Cotner and Wetzel 1992), or alternatively increased bacterial growth efficiency due to labile organic matter associated with particles could explain these results. Furthermore, high particle concentrations result in reduced light penetration and compression of the euphotic zone at a time when phytoplankton growth is keyed to light availability (Fahnenstiel *et al.* 1984, Scavia and Fahnenstiel 1987, Millie *et al.* 2002). It should also be noted that while our experimental work indicated that algal growth was stimulated by suspended sediments, the light regime in the bottle experiments would more closely represent near surface water conditions, whereas, in the lake, due to unstratified conditions, phytoplankton

are mixed considerably deeper and exposed to a lower average irradiance level.

Our present results also provide additional insight into the elevated heterotrophic production previously reported in Lake Michigan in March 1998 along a cross-shelf transect near the outflow of the St. Joseph River (Cotner *et al.* 2000). In that study bacterial production was 4.5 times greater in nearshore sites (depths < 15 m) compared to offshore, an enhancement factor quite similar to the factor of 3.9 observed in the present study (Riv+Sed treatment). As the nearshore site in the earlier study was characterized by TSM concentrations of nearly 30 mg/L, we previously concluded that this stimulation was due to the effects of resuspension. Based on the results of the present study, and the positioning of the nearshore sites near a river mouth used in that earlier study, it is clear that the stimulated BP, PP and CR was a result of the combined processes of river runoff and sediment resuspension.

### Basin-scale and Broader Impacts

Both field and experimental data indicate that despite sub-optimal temperatures and light conditions, the nearshore region is an area of intense production in the late-winter/early spring in this system, and that production levels may be keyed to large scale episodic events and variations in the amounts and distribution of river inputs. There can be large inter-annual fluctuations in both riverine input as well as resuspension events (Biddanda and Cotner 2002, Eadie *et al.* 2002, Lohrenz *et al.* 2004). The magnitude of the stimulation indicates that production that occurs within these regions over the scale of a few months may contribute significantly to fueling many food web dynamics well into the spring and possibly summer. Additional periods of resuspension are also likely in the fall once the water column has returned to an unstratified condition (Schwab *et al.* 2006).

To examine this supposition we extrapolated our experimentally determined production rates to an annual basis for both the nearshore zone and entire volume of southern Lake Michigan. For these calculations we assumed that the nearshore zone corresponds to the region less than 45 m with an average water column depth of 25 m. Furthermore we assumed annual sediment resuspension duration of 60 days per year (based on long-term climatology described by Schwab *et al.* 2006) and that the effects of riverine inputs extended to the volume of water

represented by a 20% volumetric contribution. This volume was estimated as five times the sum of the long term annual discharge measured by the USGS for the five major rivers systems in southern basin (Robertson 1997). Given these assumptions, we estimate that bacterial production within the nearshore zone is approximately 2-fold greater than background levels given the combined effects of river runoff and resuspension. For these two inputs, the effect of river runoff was about 60% greater than for resuspension. Similarly, primary production in the nearshore zone was enhanced 4.1 times over background rates, and the effect of river runoff was nearly 2.7 times greater than that of resuspension. Extrapolating these results to the entire volume of southern Lake Michigan indicated that nutrient inputs from riverine and resuspension processes accounted for 7 and 21 percent of the annual BP and PP production, respectively.

It appears that riverine inputs play a more substantial role in regulating both heterotrophic and autotrophic rate processes within the southern region of Lake Michigan than resuspension events. Results from this and other studies suggest that resuspension effects may impact heterotrophic components of the food web more than autotrophic components. This finding is consistent with the conclusion of companion field studies by Millie *et al.* (2003) and Bergmann *et al.* (2004) and in the parallel enrichment experiments of Lohrenz *et al.* (2004). Each of these studies concluded that the effects of resuspension were negligible on phytoplankton growth and photosynthetic rates within southern Lake Michigan and that resulting light limitations under ambient plume conditions limited primary production. Millie *et al.* (2003) concluded that while light-saturated growth rates did correlate with increased TSM levels, differences in metabolic processes between sediment- and non-impacted assemblages were confounded by both short-term compositional variations due to injection of meroplankton, and potential influence of nutrients from river runoff.

The magnitude of the episodic resuspension events (3,000 km<sup>2</sup>, sediment input equal to total annual river inputs) and the observed stimulus to plankton metabolism from these events and coastal runoff imply that these processes have profound impacts on the biogeochemistry and production cycles in southern Lake Michigan. While, the present study focused on southern Lake Michigan, it should be noted that resuspension events are common in the other Laurentian Great Lakes as well—especially during unstratified periods. For example,

sediment resuspension events are particularly frequent in the shallowest of the Great Lakes, Erie (Lick *et al.* 1994), where they can have significant impacts on phytoplankton composition and production (Carrick *et al.* 2005). Significant resuspension events have even been observed in the deepest lake, Superior, and less frequently in all of the other Great Lakes (Urban *et al.* 2005). The importance of coupled resuspension and riverine-fueled net production in shallow coastal regions with subsequent transport of organic matter to deeper regions for ultimate burial may be of particular significance in large lakes. In small lakes, while resuspension may occur more frequently and even during stratification, little of the increased organic matter is ultimately buried (Schelske *et al.* 1995). Nonetheless, it should be noted that the shallow nature of small lakes, and the increased light availability, perhaps would stimulate autotrophic production to a much greater extent than we observed in Lake Michigan, and perhaps more similar to what we observed in the incubation experiments. An important difference in larger systems, such as the Great Lakes is that resuspension and riverine stimulated net production can be more readily transported offshore to deeper regions where it can settle and be permanently buried (Eadie *et al.* 2002). In summary, the food web consequences and the biogeochemical implications of such late winter stimulation of production in the nearshore ecosystem and its transport to the open lake are only just beginning to be appreciated. Furthermore, potential alterations in weather patterns associated with patterns of El Nino, or long-term climate change, could have a pronounced impact on regional productivity through alterations in the timing and magnitude of both cyclonic storms that drive the resuspension events (Schwab *et al.* 2006), the timing and amount of precipitation and runoff, as well as, changes in thermal structure and mixing within the water column.

#### ACKNOWLEDGMENTS

We thank the NOAA Great Lakes Environmental Research Lab for use of the field station for the experiments and to Dr. Gary Fahnenstiel for helping plan and coordinate the study. We also thank the crew of the R/V *Laurentian* for assistance during all field sampling for the EEGLE program. This research was supported by a jointly funded program through NOAA and NSF as part of the EEGLE program (NOAA-46290000) administered through the Cooperative Institute for Limnology and Ecosys-

tems Research at the University of Michigan. Dr. Biddanda received additional support for this research from NSF grant (MIP 0603944).

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Submitted: 28 June 2007

Accepted: 19 December 2007

Editorial handling: Hunter J. Carrick